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Diversity, distribution and dispersal of Antarctic terrestrial algae

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Terrestrial algae have been studied at widespread Antarctic localities. However, their diversity is not fully known as often collections have not been made from all habitats and techniques have been inadequate for recognition of the total flora. Identifications can be unreliable and are often left at generic level. Despite this it seems that they largely comprise cosmopolitan species but at a reduced diversity relative to other regions. There is a small element of endemic species which, in general, differ only slightly from related species elsewhere. Lack of base-line taxonomic knowledge, detailed characterization of environmental factors, and application of multivariate analysis restricts our ability to define communities and interpret their distribution patterns. Examples are provided where understanding would be greatly improved by more detailed analyses. Dispersal barriers could be operating both to and within Antarctica. However, local dispersal by wind seems readily accomplished. Overcoming dispersal barriers to Antarctica, and between ice-free localities within Antarctica, could present a greater problem. Investigation of long-distance transport of propagules by wind, birds and humans is needed.

Keywords: algae; cyanobacteria; terrestrial; Antarctica; taxonomy; endemism; distribution; dispersal.

Introduction

A recent account (Pankow *et al.*, 1991) estimated that 700 taxa of non-marine algae have been recorded from Antarctica. Perhaps 200 of these occur in terrestrial habitats. Both estimates are tentative as there are major gaps in our knowledge of diversity of Antarctic algae.

This review considers the terrestrial algae of Maritime and Continental Antarctic regions (Smith, 1984; Fig. 1). They are widespread and occur at all ice-free localities so far investigated. In favourable habitats they form visible surface crusts and mats and where external conditions are unfavourable they occupy protected cryptic habitats. The flora is dominated by cyanobacteria (blue-green algae) and chlorophytes (green algae), with xanthophytes (yellow-green algae) and bacillariophytes (diatoms) as frequent associates (Table 1). They are more significant in the cold and arid Coastal and Slope Provinces of Continental Antarctica. In contrast, bryophytes and lichens dominate the vegetation in the milder and moister Maritime Antarctica (Smith, 1984).

Taxonomic studies and knowledge of distribution up to the early 1960s have been reviewed by Hirano (1965) and Koob (1967). Vincent (1988) summarizes the ecology of Antarctic terrestrial algae while Round (1981) and Hoffmann (1989) provide global overviews.

0960–3115

The descriptive phase of study is by no means complete despite having been initiated last century (Hooker, 1847), recommenced using specimens collected during the 'heroic age' of continental exploration (e.g. West and West, 1911; Fritsch, 1912) and then having regained momentum in the 1960s. Thorough knowledge of floristics is essential for underpinning research on ecological processes (Round, 1981) which is an increasing component of studies on terrestrial algae (e.g. Wynn-Williams, 1992a; Davey and Rothery, 1993; Friedmann *et al.*, 1993). This includes study of the consequences of environmental change, for instance warmer climate (Wynn-Williams, 1993) and enhanced ultraviolet radiation (Wynn-Williams, 1994).

If we are to conserve the indigenous biota then a thorough knowledge of the diversity and distribution of vegetation, including terrestrial algae, is essential (Abbott and Benninghoff, 1990; Russell and Smith, 1993). Also, detection of new colonizers would then be possible.

The distinction between aquatic (Vincent and James, 1996) and terrestrial habitats is not clear cut, and undoubtedly some overlap occurs in species distribution. Here, terrestrial algae are regarded as those that occur in situations ranging from the extremely wet, e.g. on

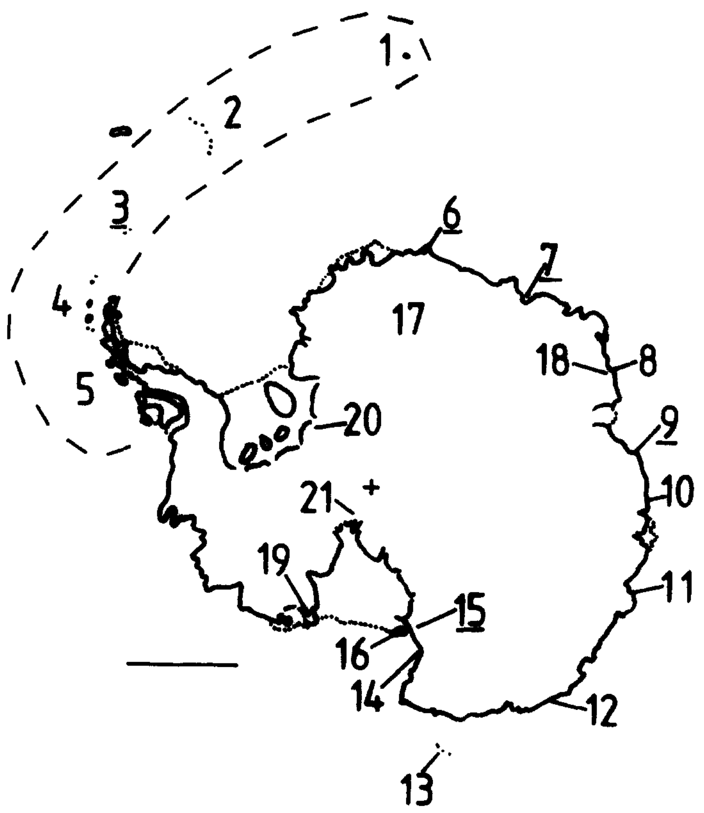

Figure 1. Map of Antarctica showing localities where there is at least some floristic description of terrestrial algae. The dashed line encloses the Maritime Region. Localities are named in Table 3. There is some detailed knowledge only for underlined localities (see text for discussion of inadequacies for even these). Scale = 1000 km at 71°S.

Table 1. Examples of genera of Antarctic terrestrial algae[a].

Cyanobacteria *(blue-green algae)*[b]	
Unicells including those in mucilaginous colonies	*Aphanocapsa, Chroococcidiopsis, Gloeocapsa, Synechococcus*
Undifferentiated trichomes[c], 'oscillatorialeans'	*Lyngbya, Oscillatoria, Microcoleus, Phormidium, Plectonema, Pseudanabaena, Schizothriz*
Unbranched chains of cells which differentiate heterocysts	*Anabaena, Calothrix, Microchaete, Nodularia, Nostoc, Scytonema, Tolypothrix*
Branched chains of cells which differentiate heterocysts	*Mastigocladus, Stigonema*
Chlorophyta *(green algae)*	
Unicells with flagella	*Chlamydomonas, Chloromonas*
Non-motile unicells	*Bracteacoccus, Chlorella, Chlorococcum, Elakatothrix*[d]*, Hemichloris, Rhopalocystis*[d]*, Pseudococcomyxa, Pseudodictyochloris*[d]*, Scotiella, Tetracystis, Trochiscia*
Non-motile unicells in mucilaginous colonies	*Coccomyxa, Diplosphaera*
Unbranched filaments	*Stichococcus, Fottea*[d]*, Hormidiospora*[d]*, Ulothrix*
Branched filaments or regular cell aggregates	*Desmococcus, Microthamnion*[d]*, Prasiococcus, Pleurococcus*
Expanded ribbons and sheets of cells	*Prasiola*
Unicellular desmids	*Actinotaenium, Cylindrocystis, Mesotaenium*
Xanthophyta *(yellow-green algae)*	
Unicells	*Botrydiopsis, Monodus*
Unbranched and branched filaments	*Heterothrix, Heterococcus*
Bacillariophyta *(diatoms)*	
Unicells	*Achnanthes, Eunotia, Hantzschia, Navicula, Pinnularia*
Pyrrhophyta *(dinoflagellates)*	
Unicells in small mucilaginous colonies	*Gloeodinium*

[a] Includes commonly recorded genera and others mentioned in the text.
[b] Nomenclature follows the 'traditional system', e.g. Geitler (1932).
[c] A trichome is a chain of adherent cells.
[d] Genera known only from Signy Island in Maritime Antarctica.

Table 2. Summary of habitats of terrestrial algae in Antarctica.

Algal community	Habitat
Lithophytic	On or within rock substrata
Epilithic	On external, exposed surfaces
Endolithic	Within diaphanous rocks, up to a few mm below the surface
Chasmoendolithic	Within fissures and cracks open to the rock surface
Cryptoendolithic	Within minute cavities inside the rock matrix
Hypolithic	On the undersurfaces of diaphanous stones lying on soils
Edaphic	On the surface of and within soils classified broadly as: (i) ahumic mineral soils (ii) biogenic soils enriched in nutrients by bird and seal activity (iii) brown earth soils which are restricted to Maritime Antarctica where they are found only below the two Antarctic vascular plants (Walton, 1984).
Epiphytic	On the living surfaces of mosses and liverworts
Cryophilic	Between ice crystals in surface layers of melting snow

and amongst bryophyte cushions bordering streams, to the extremely dry, e.g. in soils of the dry valleys of southern Victoria Land (Table 2). Although the ecological range of algae is extended by their mutualistic occurrence in lichens (Kappen 1993), it is free-living forms which are the subject here.

Adequacy of collections and analyses of samples

The compilation of a complete inventory of Antarctic terrestrial algae is dependent on the fulfilment of several criteria. There has to be adequate geographic spread of collections covering the climatic and geological diversity of Antarctica. At each locality the total range of habitats supporting algal populations must be sampled. The samples must then be observed using appropriate techniques for the recognition and reliable identification of all species within each sample. These remain to be fulfilled despite strongly stated criticism by Koob (1967).

Geographic spread of floristic studies

The spread of localities where at least some observations have been made (Fig. 1 and Table 3) indicates good geographic coverage. Latitudinal range is from the northernmost islands of Maritime Antarctica (Bouvetøya, 54° 25' S) to mountains in the Queen Maud Range (86° 13' S). Also, around the periphery of the Continent observations have been made at widely spaced localities.

Many studies have been superficial due to inadequacies in scope of collections, treatment of samples and reliability of identifications (Table 3). Anything approaching a complete species list is available for only South Orkney Islands (Broady, 1979a), Schirmacher Oasis (Pankow *et al.*, 1987, 1991), ice-free areas of Lützow-Holm Bay (e.g. Akiyama, 1967; Ohtani, 1986), Vestfold Hills (e.g. Broady, 1986) and southern Victoria Land (e.g. Seaburg *et al.*, 1979; Friedmann *et al.*, 1988). However, there are inadequacies even in these studies.

Habitat range of collections

As different habitats support the growth of different species, thorough investigation should be made of every habitat at each locality. Rarely has this been accomplished (Table 3, e.g. Pankow *et al.*, 1987, 1991). For instance, on Bouvetøya (Klaveness and Rueness, 1986), algae were examined in samples from only organically-enriched soils, wet epilithic habitats and snow. No samples were taken from extensive areas of lithosols, bryophyte communities and geothermal ground (Engelskjøn, 1981).

In southern Victoria Land there have been detailed studies of algae in mineral soils (Seaburg *et al.*, 1979) and those in endolithic habitats (Friedmann *et al.*, 1988; Nienow and Friedmann, 1993); however, there are no published reports on epiphytic or epilithic communities. These can both be found in favourably moist locations (e.g. bryophytes, Schwarz *et al.*, 1992).

Techniques employed for description of terrestrial algae

In order to identify all species of algae in any sample it is necessary to use a range of techniques (Hoffmann, 1989).

Few terrestrial algae form macroscopic growths which can be identified by their visual appearance. Two which can, *Prasiola crispa* and *Nostoc commune*, are the most frequently noted species and are often recorded in general botanical surveys (e.g. Smith, 1972; Longton, 1973).

The large majority require microscopy even where macroscopically visible crusts and mats cover the substratum. Direct microscopic examination of sample material will lead to the identification of microalgae when they are in sufficient numbers and have a distinctive morphology. All the studies reviewed by Hirano (1965) utilized only this technique, usually on preserved material.

For diatoms, where the cell walls (frustules) of dead cells are usually used for identification, it is important to verify the occurrence of living cells. Otherwise contaminating frustules dispersed from elsewhere will be included in species lists.

Enrichment cultures, e.g. soil moist plate enrichment cultures (Lund, 1945), can be used to stimulate the growth of a range of taxa and can help to reveal ones initially present only in low numbers. However, 'weed' species can be stimulated at the expense of slow-growing forms or those with more exacting growth requirements (Hoffmann, 1989).

Many terrestrial microalgae can be identified with confidence only following their isolation and thorough study in unialgal culture. This is especially true for soil algae, a fact which has been stressed repeatedly in recent reviews (Metting, 1981; Round, 1981; Starks *et al.*, 1981; Archibald, 1990). Only then can observations be made on cytological details of healthy cells, e.g. shape, position and number of chloroplasts, and stages of their life-cycles, which are often necessary for definitive identification. The first use of this approach in Antarctica was by Holm-Hansen (1964). Unfortunately, it has been adopted in too few subsequent studies.

However, there are problems. Many algae can be difficult or impossible to grow in culture. Also, all media and growth conditions are selective for particular taxa. Additionally, it cannot always be assumed that the cultured algae are active in the habitat. They may be present only in low numbers as resting stages.

In a broad-ranging study of the terrestrial algae of Signy Island, I discussed (Broady, 1979a) the success of direct examination and cultures for identification of species. A wide

Table 3. A summary of floristic studies on Antarctic terrestrial algae indicating localities, techniques applied and habitats investigated.

Locality[a]	Literature[b]	Habitats[c]							
		Epil	Endo	Hypo	Ahum	Biog	Brow	Epip	Cryo
Maritime Region									
1. Bouvetøya	Klaveness and Rueness (1986)	D+[d]	n	n	–	D+	n	–	D+
2. South Sandwich Is	Longton and Holdgate (1979)	–	n	n	D+[e]	D+	n	D+	D+
3. Signy Is,	Broady (1979a)	D++	D++	n	DEI++	DEI++	DEI++	DEI++	–
South Orkney Is	Fogg (1967), Kol (1972)	–	–	–	–	–	–	–	D+
4. South Shetland Is	Cameron and Benoit (1970)	–	n	n	E+[c]	–	–	–	–
	Broady (1979b)	–	n	n	–	EI+	–	EI+	–
	Ohtani (pers. comm.)	–	n	n	–	I+	–	I++	I++
5. Antarctic Peninsula and offshore islands	Broady (1979b),	–	n	n	EI+	EI+	EI+	EI+	–
	Corté (1966), Curl and Becker (1970)	–	–	–	–	–	–	–	D++
Continental Region									
Coastal Province									
6. Scirmacher Oasis	Pankow *et al.* (1991)	D++	D++	D++	D++	n	n	D++	D+
7. Lützow Holm Bay	Akiyama (1967)	–	–	–	E++	–	n	–	–
	Akiyama (1979)	–	–	–	–	–	n	–	DE++
	Ohtani (1986), Ohtani and Kanda (1987)	–	–	–	–	–	n	D++	–
	Ohtani *et al.* (1991)	–	–	–	D+	–	n	D+	–
8. Mawson Rock	Broady (1981b, c, 1982b)	D+	D+	n	D+	n	n	D+	D+
9. Vestford Hills	Broady (1981a, b, c, 1982a, 1986)	D++	D++	D++	DEI++	DEI+	n	DEI++	–
10. Haswell Island	Kol (1968, 1973)	–	–	–	E+	–	n	–	DE+

11. Windmill Islands	Ling and Seppelt (1990, 1993)	–	–	–	–	–	n	–	DI+
12. Point Géologie	Kol (1971)	–	–	–	–	–	n	–	DI?+
13. Balleny Islands	Kol and Flint (1968)	–	–	–	–	–	n	–	DI+
14. Terra Nova Bay	Broady (1987a),	D+	D+	D+	D+	D+	n	D+	–
	Broady *et al.* (1987)	n	n	n	DI++[e]	n	n	DI+[e]	n
15. South Victoria Land	Seaburg *et al.* (1979),	–	–	–	DEI++	n	n	–	–
	Friedmann *et al.* (1988)	n	D++	–	–	n	n	n	n
16. Ross Island	Holm-Hansen (1964),	–	–	–	DEI+	–	n	–	–
	Broady (1984),	n	n	n	DI++[e]	n	n	n	n
	Broady (1989c)	D+	D+	D+	D+	D+	n	–	D+
Slope Province									
17. Drønning Maud Land inland mountains	Engelskjøn (1986), Ryan *et al.* (1991), Pankow *et al.* (1991)	D+	D+	n	D+	D+	n	D+	–
18. Framnes Mountains	Broady (1981c)	–	D++	n	–	n	n	–	n
19. Edward VII Peninsula	Broady (1989a)	D+	D+	n	D+	D+	n	D+	n
20. Pensacola Mountains	Parker *et al.* (1982a)	n	n	n	E+	n	n	n	n
21. Queen Maud Range	Claridge *et al.* (1971), Cameron (1972b)	n	n	n	E+	n	n	n	n

[a] Regions and Provinces as recognized by Smith (1984). Figure 1 shows all localities listed.

[b] Only studies regarded as significant for a locality are included. Literature prior to 1964 is omitted.

[c] For habitat descriptions see Table 1. Epil = epilithic; Endo = endolithic; Hypo = hypolithic; Ahum, Biog, Brow = ahumic, biogenic and brown earth soils; Epi = epiphytic; Cryo = snow.

[d] Techniques: D = direct microscopic examination; E = mixed species enrichment cultures; I = isolation as unialgal cultures. Intensity of study: + = low intensity, few samples, incomplete characterization of algae: ++ = higher intensity, thorough sampling, detailed characterization of algae; n = habitat not occurring or not known to occur at locality of study; – = habitat known or likely to occur but not sampled.

[e] Heated soils from fumaroles.

Table 4. A comparison of three techniques for identification of terrestrial algae at Signy Island. South Orkney Islands[a].

Taxa	Total species	% identified		
		D[b]	M	C
Cyanobacteria	49	51 (22)[c]	69 (35)	35 (4)
Chlorophyta	64	28 (9)	44 (14)	67 (45)
Xanthophyta	17	6 (0)	41 (12)	88 (59)
Bacillariophyta	30	93 (27)	73 (7)	17 (0)

[a]Data from Broady (1979a).

[b]Techniques used were: D = direct microscopic examination of sample material; M = mixed species enrichment cultures; C = isolation of unialgal cultures.

[c]Parentheses enclose percentage of species identified only by using a particular technique.

range of chlorophytes and xanthophytes were identified only after their isolation in culture whereas cyanobacteria and diatoms were mostly identified during direct microscopic examination of samples or in mixed species enrichment cultures (Table 4). Similar conclusions resulted from a study at the Vestfold Hills (Broady, 1986).

In no region of Antarctica have terrestrial algae from all habitats been studied using a range of techniques for identification of all species (Table 3). For instance, at Signy I. (Broady, 1979a), all samples were examined by direct microscopic examination but culture techniques were used on only a proportion. None of the epilithic and chasmoendolithic material was examined using cultures and moist plate enrichment cultures were used on only 33 of the 72 samples of soils and bryophytes. Although a range of algae were isolated into unialgal cultures only one defined medium was used and hence the range of isolates was probably restricted.

Reliability of identifications

Recent reviews of algal diversity (eukaryotic algae, Andersen, 1992; cyanobacteria, Castenholz, 1992) have stressed problems with species concepts and concluded that overall, their biodiversity is not well known.

In this section our knowledge of the taxonomy of terrestrial Antarctic cyanobacteria, chlorophytes and xanthophytes is assessed. Diatoms are considered by Jones (1996, this issue).

Cyanobacteria

The systematics of cyanobacteria is beset with problems with different approaches being taken by different researchers (Castenholz, 1992). The 'traditional approach' utilizes a morphological species concept based on appearance of macroscopic growths in the field and characteristics visible down the light microscope (e.g. Geitler, 1932). This is being replaced by systems utilizing cultures, electron microscopical characters and physiological, biochemical and genetical data (e.g. Anagnostidis and Komárek, 1985; Castenholz and Waterbury, 1989).

The large majority of Antarctic studies (e.g. Seaburg *et al.*, 1979; Pankow *et al.*, 1991) apply the 'traditional approach', often comparing specimens with descriptions in early Antarctic literature (e.g. West and West, 1911; Fritsch, 1912). These descriptions are brief and were made from preserved samples. Illustrations are often inadequate. For instance, Oscillatoriales are widespread in Antarctica. Distinguishing morphological species in field material using light microscopy is often impossible. Great care has to be exercised in comparing specimens with published descriptions since species are often separated by just one morphological character. There can even be doubt regarding the limits of certain genera as diagnostic characters can be unstable. The futility of this approach with such simple cyanobacteria has been revealed by recent molecular genetical studies. These have shown strains of almost identical morphology to be phylogenetically distant (Giovannoni *et al.*, 1988).

Some researchers have been tempted into using a simplification of the traditional system (Drouet, 1981) which regards 'traditional species' as environmentally induced phenotypic variations of a few genotypes. This concept lacks a firm empirical basis (Anagnostidis and Komárek, 1985; Castenholz, 1992). Also, its application (e.g. Cameron, 1972a; Zaneveld, 1988) leads to loss of valuable information about the diversity of morphotypes when species are listed simply by their 'Drouetian' epithets.

A revision of the traditional system is in progress (Anagnostidis and Komárek, 1985, 1988) which utilizes information from cultured strains as well as from field collections. Only one study has attempted to apply this to Antarctic specimens (Broady and Kibblewhite, 1991) and it is likely to be increasingly used.

A parallel development is the taxonomic system being established by bacteriologists (Castenholz and Waterbury, 1989). This is based on cultured strains. Ideally, these will be derived from well-characterized field specimens which will help integration of traditional and bacteriological systems. There have been few attempts to isolate Antarctic cyanobacteria (e.g. Broady *et al.*, 1984). Also, it is recognized that many cyanobacteria are difficult to culture, or have never been grown (Castenholz and Waterbury, 1989). Until this is achieved, their identification will continue to be based on field specimens.

Endolithic cyanobacteria provide a useful example of the difficulties. Friedmann *et al.* (1988) described 17 cyanobacteria from the McMurdo Dry Valleys (Ross Desert). Most have not been cultured and are identified only to generic level using the traditional system. Several of their *Gloeocapsa* spp are morphologically similar to those found in epilithic communities in other regions of Antarctica (e.g. Vestfold Hills; Broady, 1981a). Also, their *Microchaete* sp is close in appearance to epilithic *Calothrix* sp described by Broady (1981). The true relationships between these entities will have to await detailed molecular genetical analysis and study of cultured strains.

The only use of molecular genetics on Antarctic strains is briefly reported by Nienow and Friedmann (1993). DNA–DNA hybridization confirmed that morphologically similar strains of *Chroococcidiopsis* from Antarctica and hot deserts belong to the same species.

The potential of culture studies has been shown in a study of endolithic bacteria by Hirsch *et al.* (1988). Their cultures revealed up to 17 different morphotypes of cyanobacteria from single 3–6 g rock samples. These need to be characterized in detail and linked to the field specimens from which each is derived.

Chlorophyta and Xanthophyta

Thirty genera of chlorophytes and xanthophytes have been recorded. However, despite a general appreciation of their diversity, many taxonomic details remain unanswered. Improvements will be made by more rigorous taxonomic studies, with greater use of cultures and molecular approaches. Detailed studies on cultured isolates have commenced (Broady, 1982a; Tschermak-Woess and Friedmann, 1984; Darling *et al.*, 1987; Chappell and O'Kelly, 1991; Broady and Ingerfield, 1993; Ling and Seppelt, 1993; Massalski *et al.*, 1994) but certainly many remain to be examined. The recent availability of a flora of world-wide terrestrial algae (Ettl and Gärtner, 1995) should stimulate future research. Examples requiring further study are given below.

Prasiola is commonly found on biogenic soils and is usually assigned to *P. crispa*. A second species, *P. calophylla*, is widespread in glacial streams in southern Victoria Land (Broady, 1989b). Separation of the two species is based largely on their characteristic thallus morphology. The former develops expanded sheets whilst the latter produces narrow ribbons attached by a basal holdfast. However, both can produce growth forms typical of the other. They might comprise a pleiomorphic species of wide ecological amplitude. The application of molecular approaches and study of cultured material would help resolve this problem.

Reliable species identifications can be made on only a small proportion of specimens during microscopic examination of field material. These include species with distinctive morphological and cytological features, such as desmids. Other identifications are usually unreliable and should be regarded as 'collective taxa', which can group together several unrelated taxa.

Additionally, life-cycle stages have been mistakenly described as independent species. Antarctic snow algae collections commonly record *Scotiella* spp (e.g. Corte, 1966; Kol, 1971; Akiyama, 1979) but culture studies have shown these to be zygotes of *Chloromonas* spp (Hoham *et al.*, 1983). Also, the red snow alga identified from field specimens as resting stages of *Chlamydomonas nivalis* at the Windmill Islands (Llano, 1965) has subsequently been found to be a new species of *Chloromonas* when examined in culture (Ling and Seppelt, 1993).

'Unidentified unicells' are often recorded by investigations using microscopic examination of field specimens (e.g. Ohtani, 1986; Broady, 1987a, 1989a; Ryan *et al.*, 1989; Ohtani *et al.*, 1991). Even when unialgal cultures are established identifications are often left at the generic level. For instance, noted often are *Bracteacoccus*, *Chlorococcum* and *Tetracystis* (e.g. Holm-Hansen, 1964; Seaburg *et al.*, 1979; Akiyama *et al.*, 1986a; Broady, 1986). Species diversity within these genera in Antarctica is unknown. Isolates from elsewhere have been placed into respectively five, 10–15 and 16 morphologically distinct species (Komárek and Fott, 1983).

Reliability of identifications can be open to doubt. Some errors have been corrected but many probably remain. The misidentification of the chlorophyte *Pseudococcomyxa simplex* as the xanthophyte *Monodus subterraneus* has been recognized (Broady, 1987b). Both are morphologically very similar and to make a distinction requires pigment or ultrastructural analysis. *P. simplex* is now known to be widespread in Antarctica. This throws into doubt records of *M. subterraneus* and other similar *Monodus* species where confirmation of those identifications has not occurred (Akiyama, 1967; Kol, 1968; Claridge *et al.*, 1971; Seaburg *et al.*, 1979).

Comparisons of terrestrial algal floras

Antarctica compared with elsewhere

There have been numerous taxonomic and floristic studies of terrestrial algae world-wide, especially of soil algae (Metting, 1981). These are generally regarded as cosmopolitan (Starks *et al.*, 1981; Archibald, 1990). A broad comparison of genera of Antarctic soil algae with those from other regions can be made using lists provided by Metting (1981) and Archibald (1990). Many have been recorded from Antarctica but there are some notable absences.

Certain taxa seem unlikely to have been overlooked because of their distinctive appearance in sample material. For instance, the filamentous cyanobacterium *Cylindrospermum* is common on soils elsewhere, while in Antarctica it has been recorded only as a human import at a research station (Broady and Smith, 1994). The rhodophyte *Porphyridium purpureum* is reported as forming gelatinous masses on soils rich in ammonium (Hoffmann, 1989); however, it has not been found in Antarctica, even on ammonia-rich biogenic soils. Other distinctive taxa absent from Antarctica are the euglenophyte *Euglena*, the xanthophyte *Botrydium* and the chlorophytes *Protosiphon* and *Trentepohlia. Protosiphon cinnamomeus* has been commonly recorded from soils of other desert regions (Round, 1981).

There is also a range of soil-dwelling coccoid genera which have not been recorded from Antarctica, e.g. the chlorophytes *Axilosphaera, Friedmannia, Neospongiococcum* and *Spongiococcum*. This might simply be due to inadequate observations as outlined above, although it is possible that their growth requirements are not fulfilled in Antarctica.

The terrestrial diatom flora of Antarctica has reduced species numbers. As studies usually employ direct examination of oxidized sample materials in order to identify diatom frustules, then lack of culture techniques should not have caused species to have been overlooked. In a detailed investigation of soil algae in Germany, Brendemühl (1949) reported the occurrence of 100 species from 24 genera. In comparison, all terrestrial habitats in Antarctica have yielded approximately 40 species from 15 genera. Only three species, *Hantzschia amphioxys, Navicula muticopsis* and *Pinnularia borealis*, are noted regularly. Terrestrial mosses alone support 47 species from 19 genera at sub-Antarctic Campbell Island (Hickman and Vitt, 1973) and 105 species from 22 genera on the Arctic archipelago of Svalbard (Beyens and De Bock, 1989).

The desmid flora is similarly impoverished. About 15 species have been recorded from all Antarctic terrestrial habitats whereas the flora of more temperate regions is richer. For instance, 38 species have been recorded from soils of the former Soviet Union (Gollerbakh and Shtina, 1969 in Gerrath, 1993). A study of epilithic communities on cliffs in North America recorded 18 species of desmids (Camburn, 1983) whereas this habitat lacks desmids in Antarctica.

Some similarities with Antarctica are notable in the few reports of arctic and alpine soil algae. It seems that both polar regions have a diminished flora. The Russian Arctic has 302 taxa compared with 2000 taxa from soils of the former USSR as a whole (Novichkova-Ivanova, 1972). A relationship with alpine soil floras is suggested by the Antarctic occurrence of two distinctive filamentous soil algae, *Heterothrix sessilis* and *Hormidiospora verrucosa* (Broady and Ohtani, unpublished observations). Elsewhere these are known only from European alpine regions (Vinatzer, 1975). A wide range of other chlorophytes and xanthophytes have been cultured only from alpine soils (Vischer, 1945; Reisigl, 1964, 1969; Vinatzer, 1975) but comparison will have to await better knowledge of related Antarctic taxa.

There is limited evidence for Antarctic endemism. Recent literature describes several new species from Antarctica based on unialgal cultures. However, these may yet be found in other regions. Also, most differ only slightly from related species in details of their morphology, e.g. the chlorophytes *Diplosphaera mucosa* and *Coccomyxa curvata* (Broady, 1982b), *Desmococcus endolithicus* (Broady and Ingerfield, 1993) and *Heterococcus endolithicus* (Darling *et al.*, 1987). This phenomenon had been noted previously by Parker *et al.* (1972) who considered that it might be due to an evolutionary divergence of algae which have recently reached Antarctica. A similar explanation was proposed for an unusual, non-heterocystous form of the cosmopolitan thermophile *Mastigocladus laminosus*, which has been found only on geothermal ground at the summit of Mt Erebus, Ross Island (Melick *et al.*, 1991).

Other new chlorophytes described from cultures differ more distinctly from their closest relatives, e.g. *Fottea pyrenoidosa*, from soil at Signy I. (Broady, 1976) and a new snow alga, *Chloromonas rubroleosa* (Ling and Seppelt, 1993).

New genera have been erected for isolates from Antarctica. *Hemichloris*, comprising a single species, *H. antarctica*, has been found only in southern Victoria Land cryptoendolithic habitats (Tschermak-Woess and Friedmann, 1984). It resembles species from *Lobosphaera* and *Chlorella* in several respects (Komárek and Fott, 1983). *Signiosphaera multinucleata*, a new genus and species from Signy Island (Broady, 1977), has been absorbed into *Pseudodictyochloris* (Ettl and Gärtner, 1987) but has been retained as a distinct species.

Problems in the taxonomy of cyanobacteria make it impossible to comment sensibly on the relationship of most Antarctic cyanobacteria to those in other regions. However, the possibility of Antarctica containing unique taxa is supported by the observation of Friedmann *et al.* (1988) that many cryptoendolithic cyanobacteria in the Ross Desert 'appear to be new to science'. This comment, together with the occurrence of *Hemichloris*, contrasts with the earlier conclusion of Horowitz *et al.* (1972) that no species able to cope with the drought and low temperatures of this region has evolved there. However, the genetic similarity of *Chroococcidiopsis* isolates from the Ross Desert with those from hot-deserts (Nienow and Friedmann, 1993) supports that contention.

Comparisons between Antarctic regions

Koob (1967) noted the lack of information from which to draw valid conclusions about distribution of Antarctic algae. This is still largely true due to different intensities of study at different locations and application of different techniques. However, there is indication of diminished diversity in Continental Antarctica compared with Maritime Antarctica. Also, within the Continental Region certain taxa seem not to be represented at nunataks and mountain ranges of the Slope Province.

Of the 85 genera recorded from maritime Signy I. (Broady, 1979a), 18 have not been found in Continental Antarctica including ones which should be distinctive enough not to have been overlooked. The latter are *Gloeodinium*, *Eunotia* and five chlorophytes: *Pseudodictyochloris*, *Rhopalocystis*, *Elakatothrix*, *Fottea* and *Microthamnion*. The latter four were not observed in a preliminary survey of higher latitude Antarctic Peninsula sites (Broady, 1979b), suggesting a diversity gradient with increasing latitude.

The most isolated and climatically extreme terrestrial habitats are found at inland mountain ranges and nunataks, the most southerly of which is Mt Howe (87° 20' S 149° 30' W). Eleven genera (Table 5) have been cultured from mineral soils and visible mats in small ponds collected in the Queen Maud Range (85–86° 45' S 146–158° W; Claridge *et al.*, 1971; Cameron, 1972b) and in the Pensacola Mountains (82° 30'–83° 30' S 48–52° W; Parker *et al.*, 1982a). Nunataks closer to the coast, in Dronning Maud Land (Engelskjøn, 1986; Ryan *et al.*, 1989) and at Edward VII Peninsula (Broady, 1989a) support a richer flora, while this increases even further at coastal locations such as the Vestfold Hills (Broady, 1986; Table 5). At Edward VII Peninsula it is intriguing that no diatoms have been found despite application of appropriate techniques for their observation.

Environmental influences on the composition of algal communities and their distribution

Floristic accounts of Antarctic terrestrial algae usually present data on species distribution between sample sites in rather crude form as either tables (e.g. Broady, 1979a) or simply as a listing, in the text, of samples in which each occurs (e.g. Pankow *et al.*, 1991).

Multivariate statistics (Digby and Kempton, 1987) have been applied to only one Antarctic investigation (Davey and Rothery, 1993) although these are regularly used for analysis of freshwater algal communities elsewhere (e.g. Robinson *et al.*, 1994). Instead, largely subjective 'communities' or 'assemblages' are sometimes suggested (e.g. Friedmann *et al.*, 1988; Pankow *et al.*, 1991) based on frequency of occurrence, and sometimes abundance, of taxa in particular habitats.

Description of the environment is often limited to visual features without any measurement of microclimate, nutrients, salinity or pH. Only studies of cryptoendolithic algae in southern Victoria Land (Nienow and Friedmann, 1993) and soil colonization on

Table 5. Comparison of numbers of genera of terrestrial algae found at inland mountain ranges and at coastal Vestfold Hills, Continental Antarctica.

	Inland mountain ranges			Coastal
Taxa	Scott Glacier and Pensacola Mountains[a]	Edward VII Peninsula[b]	Drønning Maud Land[c]	Vestfold Hills[d]
	Lat. 82–87°S	77–78°S	71–73°S	68°S
Cyanobacteria	5	8	10	18
Chlorophyta	4	6	5	24
Xanthophyta	2	0[e]	0[e]	4
Bacillariophyta	0[e]	0	4	6
Total	11	14	19	52

[a] Claridge *et al.* (1971), Cameron (1972b), Parker *et al.* (1982a).
[b] Broady (1989a).
[c] Engelskjøn (1986), Ryan *et al.* (1989).
[d] Broady (1986).
[e] Possibly overlooked because of application of inappropriate techniques.

Signy Island (Davey, 1991a; Davey and Rothery, 1992, 1993) have provided details of physico-chemical features.

The Antarctic literature suggests numerous possibilities of where environmental measurements, combined with statistical approaches to data analysis, could enhance knowledge. The following outlines these for each broadly defined habitat (Table 2).

Epilithic communities

The occurrence of epilithic algae depends on a sufficiency of moisture at the rock surface. Because of widespread aridity these communities can be uncommon or absent at certain localities.

In coastal Continental Antarctica, dark crusts dominated by cyanobacteria (mostly *Gloeocapsa* spp) occur where thin films of meltwater irrigate rock faces. This community is intolerant of saline environments. It has not been recorded from maritime Signy Island and, at the Vestfold Hills (Broady, 1981a) and Mawson Rock (Broady, 1982b), is absent from those areas which experience wind-blown sea-spray. Also, in the generally low salinity environment of Schirmacher Oasis it occurs across the entire ice-free area (Pankow *et al.*, 1991).

Where there is frequent irrigation in saline environments *Ulothrix* dominates the community, e.g. along the shoreline at Signy Island (Broady, 1979a) and Mawson Rock (Broady, 1982b), and where sea-spray is swept inland at Cape Bird on Ross Island (Broady, 1989c). Where bird influence is strong at Signy I. this community is replaced by one dominated by *Phormidium* sp and *Navicula mutica.*

At high-salinity sites where irrigation is infrequent, or perhaps moisture is gained from high atmospheric humidity, *Prasiococcus calcarius* often dominates green crusts (e.g. Ross Island; Broady, 1989c). The strong influence of salinity in controlling appearance of this species is supported by its absence from Schirmacher Oasis (Pankow *et al.*, 1991).

All these records are indicative of interactions between moisture availability, salinity and nutrients in controlling species structure of epilithic communities. However, the relative influences of these factors have yet to be understood.

Endolithic communities

Cryptoendolithic communities of high altitude inland areas of southern Victoria Land are the most thoroughly investigated terrestrial algae in Antarctica. They are reviewed in detail by Nienow and Friedmann (1993). Five communities have from one to 10 species. Community dominants are either lichens or *Hemichloris antarctica* or various cyanobacteria. Factors controlling occurrence are unclear but it is suggested that light intensity, moisture availability, pH, rock chemistry and temperature all participate.

Coastal locations support a greater diversity of chasmoendolithic eukaryotic algae. Their growth may be stimulated by the milder, moister climate and enhanced nutrient supply from seabirds. In weathered marbles of southern Victoria Land there are 10–15 species of eukaryotic algae and cyanobacteria. Particularly characteristic is *Heterococcus protonematoides.* In contrast, in gneissic rocks of Vestfold Hills and charnockites of Mawson Rock the dominant algae are *P. calcarius*, in areas receiving windblown sea-spray, and *Desmococcus* sp and *Chroococcidiopsis* sp where sea-spray does not occur (Broady, 1981c). *Chroococcidiopsis* prefers rock faces receiving occasional meltwater percolation. This differs from the *Chroococcidiopsis* community in southern Victoria Land which occurs in extreme cold and dry habitats (Nienow and Friedmann, 1993).

In pegmatite rocks at Schirmacher Oasis, Pankow *et al.* (1991) record *Aphanocapsa endolithica* as the only, but widespread, endolithic alga. This is possibly due to the generally moist, low-salinity environment.

Zonation occurs within individual communities. For instance, the lichen-dominated cryptoendolithic community contains one or two layers of free-living algae below the upper lichen layer. Also, two of the cyanobacterial communities show vertical zonation of their components (Nienow and Friedmann, 1993). Coastal chasmoendolithic communities can exhibit an inner blue-green zone comprising *Chroococcidiopsis* sp, and an outer green zone of either *P. calcarius* or *Desmococcus* sp (Broady, 1981c). The extent to which zonation is a response to moisture and light availability or to competitive interactions is unknown (Nienow and Friedmann, 1993).

Hypolithic communities

Hypolithic algae have been reported to be common only at Vestfold Hills (Broady, 1981b) and Schirmacher Oasis (Pankow *et al.*, 1991). Elsewhere, the scarcity of suitable diaphanous stones on soil surfaces makes this an unimportant habitat (e.g. Ross Island; Broady, 1989c).

Dominant taxa closely resemble those of chasmoendolithic communities. At Schirmacher Oasis, the community comprises solely *A. endolithica.* At Vestfold Hills, *Chroococcidiopsis* sp, *Plectonema* sp, *Desmococcus* sp and *P. calcarius* are the major species. Salinity, nutrient and moisture availability have a role in determining dominance. *P. calcarius* occurs under stones on biogenic soils where salts and nutrients are elevated, and *Desmococcus* sp and *Chroococcidiopsis* sp are restricted to mineral soils. The latter two taxa occur as hypolithophytes at sites where *P. calcarius* is the dominant chasmoendolithophyte (Broady, 1981b). This suggests that salinities in the latter habitat may be high while remaining relatively low in surrounding mineral soils.

At Vestfold Hills 23 species have been recorded as hypolithophytes compared with seven chasmoendolithophytes (Broady, 1986). Most of the additional species have been found in soils although soils contain an additional 31 species not found below stones.

Similar diaphanous substrata are provided by bones and teeth of seals and birds. Green crusts of chlorophytes are found on their undersurfaces if moisture conditions are favourable, e.g. at Vestfold Hills (Broady, 1986) and at nunataks on Edward VII Peninsula (Broady, 1989a). In Taylor Valley, southern Victoria Land *P. calcarius* has been found only below bones of a mummified seal (Broady, 1983).

Edaphic communities

Antarctic soils vary greatly in their physical and chemical characteristics (Walton, 1984; Campbell and Claridge, 1987). They are derived from a range of parent rock types, contain widely differing concentrations of a variety of salts, are usually extremely low in organic content but can contain high levels, are of varied texture, pH and nutrient content and can differ markedly in moisture from extreme aridity to saturation. All these factors can change greatly over short distances. Although broad response patterns of algae have been identified, as outlined below, our understanding of details of environmental influences is meagre. This is also true for soil algae world-wide as lamented by Archibald (1990).

At Signy Island (Broady, 1979a) there is a wide range in the diversity of species in mineral, brown earth and biogenic soils. Total species numbers ranged from four to 57 at individual sites. The brown earth soils contained the most diverse community with a mean of 34 species, whereas mineral soils contained a mean of 26 species. Cyanobacteria dominated both assemblages but there were also diverse chlorophytes, xanthophytes and diatoms. Counts of algae varied widely (Broady, 1979c). Cultures produced from 57 × 10^3 colony forming units (c.f.u) cm^{-2} on a recently exposed moraine, to 13 900 × 10^3 c.f.u cm^{-2} in a brown earth soil. One of seven different chlorophytes and xanthophytes dominated the count in each of 17 soils examined.

Mineral soils on fellfields at Signy Island are the only Antarctic soils where detailed studies of algal ecology have been initiated. Epifluorescence microscopy has shown algae to be primary colonizers of soils recently exposed by ice recession. They bind soil particles and increase stabilization of mineral fines (Wynn-Williams, 1992a, 1993). Considerable spatial variation in taxa exists between frost-sorted polygons despite little variation in environmental factors being detected (Davey, 1988; Davey and Rothery, 1993). Also, different taxa have different distribution patterns across individual polygons (Davey and Clarke, 1991). Seasonal periodicity occurs. Filamentous chlorophytes dominate in early spring and filamentous cyanobacteria in summer (Davey, 1991a). Cessation of growth in late summer has been attributed to nitrogen-limitation (Davey and Rothery, 1992). Experimental studies suggest that the more effective colonizers have a good ability to attach to substrata (Davey *et al.*, 1991), and to survive repeated freeze-thaw cycles and desiccation (Davey, 1989, 1991b).

At Vestfold Hills (Broady, 1986) mineral soils flushed by meltwater support visible mats of cyanobacteria which, at different sites, are dominated by different species. Although *Nostoc commune* is common, other dominants are *Nodularia harveyana*, *Scytonema myochrous*, *Calothrix parietina* and *Tolypothrix tenuis*. Most mats also contain abundant oscillatorialean filaments. Colonial unicellular *Gloeocapsa* spp are prominent only where salinity levels are low. Where soils are moist but not flushed, oscillatorialeans dominate and heterocystous cyanobacteria are absent. This community is a colonizer of moraines at the edge of the Polar Ice Cap. It is similar to communities recorded from equivalent habitats at Schirmacher Oasis (Pankow *et al.*, 1991).

The degree of water-flushing also affects the composition of communities on biogenic soils. Irrigated soils support *Prasiola crispa* and dark mats of *Oscillatoria* sp, whereas moist soils contain diverse communities of microscopic chlorophytes. Both have *Navicula muticopsis*. Similar distribution patterns occur at coastal locations of northern Victoria Land (Broady, 1987a).

Macroscopic growths at Ross Island are influenced by salinity (Broady, 1989c). *Nostoc commune* occurs almost solely in areas not swept by windblown sea-spray. In contrast to Vestfold Hills, other heterocystous forms are lacking. Oscillatorialean mats occupy zones with and without sea-spray. Whether these contain different taxa in the different zones has not been investigated.

The strong selective effect of environmental factors is emphasized by occurrence of distinct communities on heated fumarolic ground at the summits of Mt Erebus, Ross Island (Broady, 1984), and Mt Melbourne (Broady *et al.*, 1987) and the newly discovered Mt Rittmann (Bargagli *et al.*, 1996), northern Victoria Land. Xanthophytes and diatoms are absent from all of these and there is a preponderance of unicellular chlorophytes. This is possibly a reflection of the somewhat acidic reaction of the soils. These are also the only Antarctic sites with the thermophilic cyanobacterium, *Mastigocladus laminosus*.

In the Continental Region few studies have addressed details of soil algal ecology. Quantitative studies at Lützow-Holm Bay ice-free areas have demonstrated the importance of a relatively high water availability for the occurrence of diverse and abundant algae (Akiyama *et al*., 1986a; Ohtani *et al*., 1991). Populations were also stimulated by nutrients from bird colonies although biogenic soils from the centre of colonies contained substances which prevented algal growth (Akiyama *et al*., 1986b).

Soil algal ecology in the dry valleys of southern Victoria Land was pioneered by Cameron (e.g. Cameron, 1972a, c). Physico-chemical characteristics of soils, particularly at extremely arid sites, were related to abundance and diversity of soil microbes, including algae. Unfortunately the value of these studies was reduced by the use of an inappropriate taxonomic system for the cyanobacteria (Drouet, 1981). However, conditions favourable for development of algal communities were ascertained. Particularly important is a sufficient duration of good quality water of relatively low conductivity at sites with a northern exposure which receive maximum insolation during the short summer.

Our recent studies (Broady and Smith, unpublished observations) have confirmed that at moist sites visible growths of diverse cyanobacteria and eukaryotic algae can develop. Dark crusts and mats of cyanobacteria form on valley-sides where snow accumulates over winter and melts in summer. These are dominated by *Gloeocapsa* spp, *Microcoleus vaginatus* and other oscillatorialeans. Moisture supply is probably of very short duration as most crusts were desiccated when observed.

Valley floors are generally extremely arid and devoid of visible vegetation. Using cultures, Cameron (1972c) detected algae in only one soil in Victoria Valley. However, we observed microscopic communities to be widespread in depressions bordering frost polygons. In contrast to valley side communities these are dominated by *Botrydiopsis*. These observations contrast with the contention by Horowitz *et al*. (1972) that microbes in arid soils of the dry valleys do not grow there but are carried in by winds from more favourable environments.

Epiphytic communities

All Antarctic bryophytes support epiphytic microalgae which extend below the photosynthetic tissues into the dead organic matter below. The diversity and abundance of algae varies markedly between different bryophytes.

On Signy Island, South Orkney Islands, (Broady, 1979a) a comparison was made between dry moss-cushion fellfield, moist moss turf, and wet bryophyte communities. Sites supported means of seven, 16 and 26 species respectively. In moss turf, cyanobacteria and diatoms were rarely encountered whilst they were common in wet bryophytes and of intermediate occurrence in dry moss-cushions.

A detailed examination was made at two contrasting sites, a moss turf (Broady, 1977) and a moss carpet (Broady, 1979d). Counts using culture techniques showed *Pseudococcomyxa simplex* to dominate populations in the moss turf. However, there were marked differences in numbers between the two moss species which comprised the turves, while patches of bare peat supported even greater populations. In contrast, moss carpet populations were dominated by filamentous and coccoid cyanobacteria, *Eunotia fallax*, and a variety of chlorophytes and xanthophytes of which *P. simplex* was usually a minor constituent. Horizontal variation in diversity and numbers of algae was apparent between different species of moss and liverwort. Zonation patterns were identified in the vertical distribution of algae along individual moss stems.

In Continental Antarctica, floristic accounts of epiphytic communities have been provided for Lützow-Holm Bay area (Ohtani, 1986; Ohtani and Kanda, 1987), Vestfold Hills (Broady, 1986) and Schirmacher Oasis (Pankow *et al.*, 1991). Crust-forming communities are generally dominated by cyanobacteria. *Stigonema minutum* is dominant at Schirmacher Oasis, in contrast to *Nostoc* sp and oscillatorialeans at Vestold Hills. Other genera regularly recorded in crusts, are *Gloeocapsa, Calothrix, Scytonema* and *Tolypothrix*. Where there is salt efflorescence or nutrient supply from birds the cyanobacteria can be replaced by green crusts of chlorophytes (Broady, 1986).

The absence of diatoms amongst certain moss species has been attributed to their being subjected to severe desiccation, whereas more diverse communities appear to be a response to greater moisture and nutrient availability (Ohtani, 1986; Ohtani and Kanda, 1987).

Mosses are the most favourable habitat for the few species of Antarctic terrestrial desmids, *Actinotaenium cucurbita* being recorded most frequently. These appear to be a hardy component of a richer aquatic desmid flora. For instance, at Yukidori Valley, Lützow-Holm Bay, two desmids occur amongst terrestrial mosses whereas an additional nine inhabit ponds and streams (Ohtani, 1986).

Zonation has also been noted amongst mosses in Continental Antarctica. Matsuda (1968) reported surface crusts of *Gloeocapsa* spp damaging mosses and restricting the occurrence of *Pinnularia* sp. This was more abundant in healthy adjacent moss lacking encrustations. Similarly, Broady (1982b, 1987a) found filamentous cyanobacteria to encrust the tops of raised moss hummocks, whereas in the depressions between, microscopic growths of either *Pinnularia borealis* or *Actinotanium cucurbita* were dominant.

Cryophilic communities

Snow algae are largely restricted to Maritime Antarctica and the coastal fringe of Continental Antarctica despite the region being over 98% snow- and ice-covered. Furthest south records are at 76° 34' S on Ross Island (Broady, 1989c). The furthest inland record is at nunataks in Dronning Maud Land (Ryan *et al.*, 1989) which are separated from the open ocean by 130 km of ice shelf. Even at the coastal fringe, snow algae are absent over extensive areas of snowfields. An important requirement for growth is the presence of meltwater percolating through the upper layers of snow (e.g. Ishikawa *et al.*, 1986; Ling and Seppelt, 1990, 1993). A few studies have noted patterns in species distribution which appear to depend on snow chemistry.

At Windmill Islands ice-free area, three communities have different distribution patterns. Grey snow dominated by *Mesotaenium berggrenii* (Ling and Seppelt, 1990) and red snow dominated by *Chloromonas rubroleosa* (Ling and Seppelt, 1993) are widespread on mainland ice-free areas but are very rare on offshore islands where green snow occurs around the large penguin rookeries. Preliminary chemical analyses suggest that both *C. rubroleosa* and *M. berggrennii* are adapted to snow with low conductivity and nutrient levels. Both these factors are probably substantially higher in green snow areas on the islands.

Other studies have also noted the occurrence of green snow in nutrient-enriched areas near birds (Broady, 1989c; Ryan *et al.*, 1989) and seal carcasses (Ishikawa *et al.*, 1986) although red snow also occurs (Akiyama, 1979). At Schirmacher Oasis, which has no penguin colonies and is separated from the open sea by 80 km of ice-shelf, snow algae are rarely encountered (Pankow *et al.*, 1991). However, four sites each supported distinctly different communities. The reasons for this diversity are unexplained.

A similar habitat is provided by terminal ice-walls of glaciers in dry valleys of southern Victoria Land. Foliose thalli of *Prasiola calophylla* are found in meltwater percolations where slopes are relatively gentle (Broady, 1989b). However, not all such sites support algae. Limiting factors are unknown.

Dispersal of terrestrial algae

Before an alga can establish an active population at a particular site it has to be dispersed there in a viable condition. Local airborne dispersal seems to be easily achieved, however, transport over long distances may present more problems.

Local dispersal

Several methods have been used to detect airborne algae at ice-free localities. Sticky slides exposed close to ground level at Cape Hallett, northern Victoria Land (Rudolph, 1970) captured single cells and fragments of algal thalli, moss and lichen. At Signy Island, Broady (1979e) cultured a range of local terrestrial algae on agarized medium exposed to the air. In the dry valleys of southern Victoria Land the release and wind dispersal of large freeze-dried portions of benthic mat from lakes and ponds is well known (Parker *et al.*, 1982b) and has been postulated to be a source of propagules for inoculation of soils (Wharton *et al.*, 1985). Simple 'Tauber traps' with apertures exposed at about 10 cm above the ground on the McMurdo Ice Shelf captured fragments of cyanobacterial mats (Hawes, 1991). Their origin was the extensive mineral soils and ponds on the ice shelf surface. Six genera of typical soil algae were cultured from trapped material. At the same locality, particle collectors with a large air throughput captured far fewer algae. This may be due to inadequacies of the equipment or failure to expose collectors during periods of strongest winds, a time when highest numbers of airborne particles would be expected (Hawes, 1991; Broady and Smith, 1994).

As abundant species are likely to produce more airborne propagules, the relative abundance of species could be important in determining their success in colonizing new substrata. Davey and Rothery (1993) found the most widely occurring taxa on Signy Island soils to be those which occurred most frequently as colonizers of recently exposed soil polygons.

Long-distance dispersal

Distribution to Antarctica and between ice-free localities involves long distances. Antarctica is separated from more temperate regions by wide expanses of ocean. Ice-free localities within Antarctica are effectively islands of rock in a sea of ice and can be hundreds of kilometres from their closest neighbour. Dispersal across these barriers could be by air currents, birds or humans.

Presently we have no knowledge of the abundance or identities of viable propagules of algae in the air above these sea and ice barriers. However, there is circumstantial evidence that the barriers have been, and are being, crossed.

At the last glacial maximum, about 18 000 years BP, most present ice-free areas were probably almost entirely ice-covered, for instance the South Orkney Islands (Smith, 1990) and Vestfold Hills (Adamson and Pickard, 1986). Following glacial retreat, algal communities would have developed from viable propagules deposited on newly exposed substrata. Some of these might have derived from refugia within Antarctica, such as ponds on the northern fringes of ice-shelves (Vincent, 1988) and rock exposures which remained ice-free throughout the Pleistocene glaciations, for instance areas of southern Victoria Land dry valleys (Claridge and Campbell, 1987). However, many could have come from regions to the north, resulting in the present largely cosmopolitan flora.

Favourable movement of air masses from north to south does occur (Wynn-Williams, 1991). Evidence that these transport propagules is provided by the rare occurrence of exotic mosses in cultures of Maritime Antarctic soils and the presence in firn snow of pollen grains from numerous South American phanerogams (Smith, 1993).

Long distance dispersal of algae is suggested by the presence of thermophilic *Mastigocladus lamonosus* on fumarolic ground at the summits of Antarctic volcanoes (Broady, 1993). Closest known occurrences outside Antarctica are in geothermal areas of New Zealand. Eruptions of the Antarctic volcanoes in recent centuries would probably have destroyed any earlier biota and recolonization by propagules from outside the region would then be required. As world-wide propagule sources of this alga are scattered and of small extent, then few would be expected to become airborne. The chances of these reaching the extremely small areas of Antarctic fumaroles must be very low.

The discovery of diatom frustules in deep ice taken from a remote location on the Antarctic Ice Cap (Ram *et al.*, 1988) also demonstrates the potential for long-range dispersal. However, the unusual absence of diatoms from nunataks on Edward VII Peninsula (Broady, 1989a) suggests that diatoms might lose viability during dispersal within Antarctica.

The low diversity of desmids in Antarctica has been attributed to an absence of suitable habitats (Hirano, 1965). However, Parker *et al.* (1972) noted that their airborne dispersal to Antarctica could be restricted, while agreeing that the region lacks their preferred acidic waters. They cite Schlichting (1969) as reporting the absence of desmids among nearly 200 species of viable airborne algae isolated from temperate and tropical regions. Also, Gerrath (1993) noted only occasional reports of airborne desmids. Perhaps Antarctic species are among the few members of this large group which are able to survive aerial dispersal.

Viable algae have been detected on birds migrating to Antarctica. Birds were captured over the Weddell Sea (Schlichting *et al.*, 1978) and nine chlorophyte and cyanobacteria species developed in cultures from washings.

Humans have been shown to be dispersal agents. Soil traces on fresh vegetables imported to Scott Station on Ross Island from New Zealand contained a range of taxa, including *Cylindrospermum* and *Eustigmatos* which are unknown as Antarctic indigenes (Broady and Smith, 1994). In New Zealand, abundant and diverse algae were found on equipment awaiting despatch to Antarctica, and on the boots of expeditioners boarding aircraft.

Possible directions for future research

We remain ignorant of terrestrial Antarctic algae in several areas of interest. The relationship of the flora to that of other world regions, and the existence of phytogeographic patterns within Antarctica, are unclear. Whether Antarctica is still being colonized by additional species transported by natural vectors from regions to the north is unknown. Barely considered is the extent to which the human vector might add to this process. Advice cannot be confidently proffered on how to achieve the conservation of the full diversity of algal species and communities within the evolving protected area system (Smith *et al.*, 1994). Progress is primarily dependent on improved understanding of algal taxonomy and distributional ecology.

More detailed studies at localities already collected would greatly increase known species, as has been found for lichens and bryophytes in floristically rich Maritime Antarctica (Russell and Smith, 1993). Exact recording of sample sites on large-scale maps and in geographic information systems would allow future recovery of algae of particular interest.

However, little further progress can be made without the greater utilization of cultures in conjunction with direct microscopic examination of collections. This has been stated in the Antarctic literature for over 25 years (Koob, 1967; Parker *et al.*, 1972). Superficial analyses of partial collections from previously unvisited localities are unlikely to add significantly to our knowledge.

There is a need for an up-to-date check list of all Antarctic records. The most recent, by Prescott (1979), covers literature up to 1977. A new list would usefully be annotated with assessments of the reliability of each identification, synonymy, and literature sources for descriptions and illustrations of Antarctic specimens. This would bring attention to, and facilitate the study of, problematical taxa.

Improved communication between Antarctic researchers would greatly aid in developing a reliable taxonomy. Such a community of phycologists would be best established within the framework of the international 'Biological Investigations of Terrestrial Antarctic Systems' programme (BIOTAS; Smith and Wynn-Williams, 1992). Exchange of field specimens, cultured strains, preserved material and notes and illustrations would help prevent a proliferation of different names being applied to the same alga due to different opinions as to its identity. Ideally there would be a central repository for all these resources. The values of such a repository would be similar to those elaborated by Russell and Smith (1993) for the herbarium of the Antarctic Resource Centre of the British Antarctic Survey.

The literature contains repeated reference to the undoubted influences of moisture and nutrient availability, pH and salinity on the species composition and distribution of algal communities in all terrestrial habitats. However, details of their individual effects and interactions are poorly known. Also, other factors such as competitive exclusion have not even been considered.

There have been very few attempts at characterization of the environment in which the algae exist. The importance of this is clearly demonstrated by the studies on cryptoendolithic communities (Nienow and Friedmann, 1993) where variations in light, moisture and temperature over the millimetre scale profoundly affect distribution patterns. Measurements of a range of physico-chemical factors at this scale within the living space of algal communities would enable correlation with floristic data. This needs to be achieved in all terrestrial habitats.

Measurements could usefully be made along putative environmental gradients where changes in community composition have been noted. These might operate over short distances, e.g. from the summit of a moss hummock to an adjacent depression, or larger distances, e.g. from a sea-spray swept saline area into an area free of such influence.

Understanding could also be furthered by an experimental approach. Soils in particular would be good subjects for manipulation in the field followed by analysis of algal responses. Moisture, nutrients and salinity are all readily changed, either singly or in combination, in small trial plots. The use of cloches by Wynn-Williams (1993) has clearly demonstrated their utility for increasing microclimate temperatures. Different cloche designs, e.g. UV-transparent and opaque plastics, walled and unwalled cloches, can be used to influence different factors (Wynn-Williams, 1992b). Greater control of factors could be achieved by use of laboratory microcosms, for instance by making selected amendments to Antarctic soils in controlled environment incubators.

Additionally, responses of unialgal cultures to factors such as salinity and nutrients would help interpretation of field observations. However, there is increasing realization of the variability in responses in physiological parameters between clones of single species, even when these are isolated from the same location (Wood and Leatham, 1992). Diversity at this level, and its ecological importance, has yet to be investigated in Antarctic terrestrial algae. Only the use of cultures will make this possible.

Discussion of the importance of research on propagule dispersal to Antarctica is provided by Walton (1990) and Wynn-Williams (1991). Smith (1993) presented evidence for long-distance airborne dispersal of spores of exotic bryophytes to Maritime Antarctica and their retention of viability in the soil propagule bank. Presently we lack direct evidence for both these processes in terrestrial algae.

There is a need to collect airborne propagules at remote locations. Sites on the Antarctic Ice Cap and over the Southern Ocean would be distant from contamination by dispersal of local Antarctic-derived propagules. This should enhance opportunity to detect exotic spora. Deployment of apparatus on aircraft supplying research stations would enable collection along high altitude north-south transects (Lacey and McCartney, 1992).

Birds and humans as dispersal vectors have received minimal attention. More extensive sampling of birds over the Southern Ocean coupled with analysis of migration routes, feeding areas and other factors must be considered before their importance can be established (Walton, 1990). Undoubtedly scientists and tourists visiting Antarctica transport propagules of exotic algae. Their diversity has yet to be fully investigated.

The recognition of which algae might be present in soils solely as dormant but viable propagules is a major problem. How can these be distinguished from ones present in low numbers but active? Viable exotic propagules might be more easily detected by examination of particles extracted from surface ice taken from remote locations. Abyzov (1993) has achieved this for fungi and bacteria in ice from deep cores but has not been able to culture algae (pers. comm. S.S. Abyzov).

Algae could be experimentally tested for their ability to survive conditions which they would be expected to experience during long distance airborne dispersal and on arrival in Antarctica (Vishniac, 1992). A comparison of species both known and unknown from Antarctica would suggest which of the latter had the potential to disperse and colonize.

It is clear that Antarctic terrestrial algae offer the potential for stimulating and creative research both in the field and laboratory.

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